



Temporal and spatial variation in habitat selection and movements of female mallards in the parklands of Canada

by Philip Pendleton Thorpe, Jr

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biological Sciences

Montana State University

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Abstract:

Little is known about habitat selection, size of area used, or number of wetlands used by female mallards (*Anas platyrhynchos*) during the breeding season. Less is known about how or if selection changes during different periods of the breeding season (e.g., egg development versus nesting stages). Therefore, I studied habitat use and availability on 2 different landscapes in the prairie-parkland region of Canada with the objectives of estimating habitat selection, movement patterns, and home ranges of female mallards during the different phases of the breeding season. Using radio telemetry, I collected 7,102 locations on 57 female mallards from April to August 1994-95. Habitat selection was calculated during pre-nesting, egg-production, and post-breeding periods. Home ranges were calculated for similar periods using the adaptive-kernel method. Females used an average of 6.7 to 15.3 wetlands during different reproductive periods at the 2 study areas. During all periods, uplands were used 39-49% of the time at Davis, and 12-27% of the time at Shoal Lake. Among upland habitats, cropland was used most (4-26%) on both study areas. However, females spent most of their time (57-89%) in wetland habitats, particularly semipermanent/permanent wetlands (26-49%) during all periods and on both study areas. Seasonal wetlands were used more at Shoal Lake (16-34%) than at Davis (8-11%). At Davis, high densities of tilled, seasonal, and semipermanent wetlands were available, and I found that pre-nesting and egg-producing females preferred these wetland classes and did not prefer any one wetland class more than another ($P < 0.05$). In contrast, at Shoal Lake, when only seasonal wetlands were available in high densities, pre-nesting and egg-producing females preferred seasonal wetlands significantly more than wetlands with lower densities ($P < 0.05$). At Shoal Lake, post-breeding females preferred riverine habitat among other wetland habitats. All upland habitat types were used less than expected when compared with availability ($P > 0.05$). The average 100% home range size did not differ among reproductive periods within years ($P > 0.35$). However, during the pre-laying period, 100% home range size was larger at Shoal Lake ($P = 0.005$) than at Davis. Core areas (50% home range sizes) during all periods were larger at Shoal Lake ($P = 0.004$) than at Davis. Findings suggest that mallards are habitat generalists that are variable in terms of the number and type of wetlands they use. Although sizes of average home ranges did not vary much between sites or among periods, spatial aspects of areas used by individual females were highly variable. Habitat management plans should acknowledge this variation by preserving/managing for high wetland densities and maintaining/increasing wetland diversity. Future multiple-year studies are needed to better understand habitat selection and movements for female mallards. In addition, multivariate studies involving age, wetland variables, and invertebrate population data should be conducted to provide further insight on female habitat selection and movement pattern decisions.

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MOVEMENTS OF FEMALE MALLARDS IN THE PARKLANDS OF CANADA

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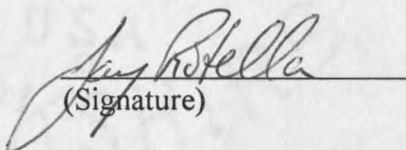
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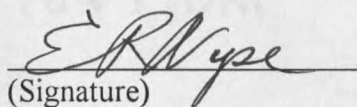
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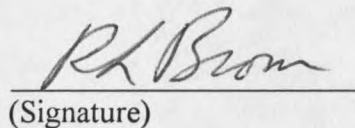
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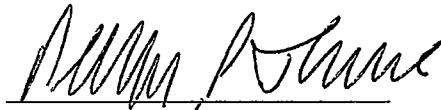
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ABSTRACT

Little is known about habitat selection, size of area used, or number of wetlands used by female mallards (*Anas platyrhynchos*) during the breeding season. Less is known about how or if selection changes during different periods of the breeding season (e.g., egg development versus nesting stages). Therefore, I studied habitat use and availability on 2 different landscapes in the prairie-parkland region of Canada with the objectives of estimating habitat selection, movement patterns, and home ranges of female mallards during the different phases of the breeding season. Using radio telemetry, I collected 7,102 locations on 57 female mallards from April to August 1994-95. Habitat selection was calculated during pre-nesting, egg-production, and post-breeding periods. Home ranges were calculated for similar periods using the adaptive-kernel method. Females used an average of 6.7 to 15.3 wetlands during different reproductive periods at the 2 study areas. During all periods, uplands were used 39-49% of the time at Davis, and 12-27% of the time at Shoal Lake. Among upland habitats, cropland was used most (4-26%) on both study areas. However, females spent most of their time (57-89%) in wetland habitats, particularly semipermanent/permanent wetlands (26-49%) during all periods and on both study areas. Seasonal wetlands were used more at Shoal Lake (16-34%) than at Davis (8-11%). At Davis, high densities of tilled, seasonal, and semipermanent wetlands were available, and I found that pre-nesting and egg-producing females preferred these wetland classes and did not prefer any one wetland class more than another ($P \leq 0.05$). In contrast, at Shoal Lake, when only seasonal wetlands were available in high densities, pre-nesting and egg-producing females preferred seasonal wetlands significantly more than wetlands with lower densities ($P \leq 0.05$). At Shoal Lake, post-breeding females preferred riverine habitat among other wetland habitats. All upland habitat types were used less than expected when compared with availability ($P > 0.05$). The average 100% home range size did not differ among reproductive periods within years ($P \geq 0.35$). However, during the pre-laying period, 100% home range size was larger at Shoal Lake ($P = 0.005$) than at Davis. Core areas (50% home range sizes) during all periods were larger at Shoal Lake ($P = 0.004$) than at Davis. Findings suggest that mallards are habitat generalists that are variable in terms of the number and type of wetlands they use. Although sizes of average home ranges did not vary much between sites or among periods, spatial aspects of areas used by individual females were highly variable. Habitat management plans should acknowledge this variation by preserving/managing for high wetland densities and maintaining/increasing wetland diversity. Future multiple-year studies are needed to better understand habitat selection and movements for female mallards. In addition, multivariate studies involving age, wetland variables, and invertebrate population data should be conducted to provide further insight on female habitat selection and movement pattern decisions.

INTRODUCTION

The prairie-parkland region of south-central Canada is the most important production area for mallards in North America (Bellrose 1980, Anonymous 1994). In 1996 alone, aerial surveys estimated that 46% of the continental breeding mallard population was in Manitoba, Saskatchewan and western Ontario (Canadian Wildlife Service [CWS] and U.S. Fish and Wildlife Service [USFWS] 1996).

Mallards are attracted to the prairie-parkland region of Canada because of its high density and diversity of wetlands. Wetlands provide female mallards with: nutrition required during egg development, isolation for pair bonding, escape cover, and resting and staging areas during molt and fall migration. Accordingly, Pospahala et al. (1974) found a strong positive relationship between the number of prairie-parkland wetlands present in May and the size of the mallard breeding population in the prairie-parklands during the same year.

Despite the demonstrated importance of wetlands to breeding ducks, over 50% of the original wetlands in the prairie-parkland region of Canada have been destroyed by agriculture (Anonymous 1994:143). Further, 59% of the remaining wetland basins and 79% of the remaining wetland margins have been impacted by human disturbance (Turner et al. 1987). Wetlands with water permanencies of short duration (e.g., ephemeral and temporary wetlands, Stewart and Kantrud 1971) have been affected to a greater extent than more permanent wetlands. For example, in the parkland region of Canada, 61% of

ephemeral and temporary wetlands have been negatively affected by humans (e.g., cultivated), as compared to only 22% of seasonal and semipermanent wetlands (Turner et al. 1987). The extensive loss of shallow wetlands (i.e., ephemeral and temporary) may be detrimental to mallards. Ephemeral and temporary wetlands are thought to be biologically important to female mallards because, given their shallow nature, they melt earlier than other wetland types and, therefore, may have invertebrate populations that become available to mallards earlier in the breeding season (Swanson et al. 1985). Deeper wetlands, which thaw later, may not become critically important to breeding mallards until later in the season. Late in the season most shallow wetlands are dry, which may make more permanent wetlands a critical habitat feature during nesting and/or post-nesting periods.

Uplands, which provide for nesting, have also been impacted heavily by agricultural activities. Native upland grasslands have disappeared at a rate of 2% per year (CWS and USFWS 1986). Baydack et al. (1995) estimated that only 20% of the native Canadian prairie landscape remains. Most mallard nests are in upland habitats, and low nesting success and recruitment rates have been attributed to degradation of upland habitats and changes in predator communities (Cowardin et al. 1985, Greenwood et al. 1987, Sargeant et al. 1993).

Given high levels of habitat loss and its potential impacts on duck populations, the North American Waterfowl Management Plan (NAWMP) was developed (CWS and USFWS 1986). The NAWMP states that the first priority in waterfowl management should be to perpetuate waterfowl populations and their supporting habitats and to

encourage the optimum use of available habitats. The NAWMP implements these goals on a regional level through joint ventures. The Prairie Habitat Joint Venture (PHJV) is the largest of the NAWMP's joint venture programs and is dedicated to improvement of waterfowl habitat in the prairie-parklands of Canada (Anonymous 1987, see CWS and USFWS 1994). The PHJV targets habitat improvements on areas with high densities of wetlands and breeding mallard pairs. However, little is known about the importance of individual wetland classes to mallards in the areas managed by the PHJV. Given the high loss of ephemeral and temporary wetlands in Canada, even target areas with high wetland densities may not include all wetland classes preferred by mallards. The PHJV assumes that the major problem for prairie-nesting ducks is the lack of secure and attractive nesting habitat and, therefore, focuses strongly on improving upland nesting habitat. While studies have been conducted (e.g., Greenwood et al. 1987, see Clark and Nudds 1991) or are underway regarding which upland habitat types are most appropriate to create, little is known regarding appropriate spatial arrangements of habitat treatments. In particular, it would be useful to know how to optimally disperse treatments across a landscape to ensure that all birds are exposed to quality nesting habitats.

Previous studies in the prairie-parkland region provide some, but not all, of the information needed for managing habitat for breeding mallards. Although many studies have examined nest-site selection (e.g., Kirsch et al. 1978, Cowardin et al. 1985, Klett et al. 1988, Greenwood et al. 1995), few have investigated non-nesting aspects of habitat selection and movements by mallards. Further, the few studies (Stoudt 1971, Stewart and Kantrud 1973, Kantrud and Stewart 1977, Duebbert et al. 1983, LaGrange and Dinsmore

1989) of female mallard habitat use conducted during the pre-nesting and nesting periods have not related use to availability. Only Dwyer et al. (1979) and Mulhern et al. (1985) have incorporated availability data and estimated habitat selection in the prairie-parkland region of North America. A similar lack of knowledge exists about habitat requirements of post-nesting females. Although researchers have investigated habitat use/selection by broods (Ball et al. 1975, Talent et al. 1982, Orthmeyer and Ball 1990, Krapu and Luna 1991), only 1 study (Rotella and Ratti 1992) was done in the parkland region of Canada. No studies have been done on habitat selection by females that failed to produce ducklings. Only 2 studies (Dzubin 1955, Dwyer et al. 1979) have been done that provide information regarding optimal spatial arrangement of habitats (e.g., home range studies) in the prairie-parkland region.

Therefore, although the PHJV has/collects nest-site data, it does not have adequate data regarding other aspects of the habitat requirements of mallards. Furthermore, inferences from the few studies of non-nesting habitat use and/or selection that have been conducted in the prairies (Stewart and Kantrud 1973, Dwyer et al. 1979) may not apply well to the parklands. Habitat use by breeding mallards may be quite different in the prairies and parklands because the 2 areas differ in mallard densities, wetland densities, and landscape composition. Thus, data are clearly needed regarding the types of upland and wetland habitats that are important to female mallards in the parklands. Also, movement data would provide information regarding optimal spatial arrangements of habitat treatments. Therefore, I examined habitat use and availability on 2 different landscapes in the parkland region of Canada during key phases of the breeding season to

achieve the following objectives: (1) estimate habitat selection, (2) describe movement patterns, and (3) estimate home range sizes during each reproductive period.

STUDY AREA

I conducted research on 2 study areas (one in Saskatchewan, one in Manitoba) in the prairie-parkland biome (Poston et al. 1990) (Figure 1). Each study area (12.8-20.5 km²) was part of a larger study area (64 km²) being used by the PHJV Assessment Program (PHJV Proposed Assessment Study Design, Ducks Unlimited's Institute for Wetland and Waterfowl Research [IWWR], Stonewall, Manitoba, unpublished report, 1991) to evaluate nesting success, nest-site selection, and recruitment of female mallards on control and treated areas (0-20% of the landscape affected by PHJV habitat programs). Two different study areas were chosen to examine spatial variation in habitat preference and home range size. The sites were selected based on wetland densities and anticipated breeding pair populations and were located in areas that are/will be targeted for PHJV habitat treatments. Logistical constraints prevented me from working on both areas in each year. Also, working on 2 different study areas in 2 different years confounded the effects of space and time on results. However, I concluded that the benefits of obtaining a broader measure of spatial variation in parameters of interest outweighed the difficulties of data interpretation resulting from the unreplicated design.

The Davis study area (12.8 km²) was located 6 km southeast of Prince Albert, Saskatchewan (53° 9' N, 105° 37' W) in the Red Deer Hills subregion of the parkland ecoregion (Poston et al. 1990). Topography was gently rolling, and the area contained numerous and diverse wetlands of all permanency classes (Stewart and Kantrud 1971)

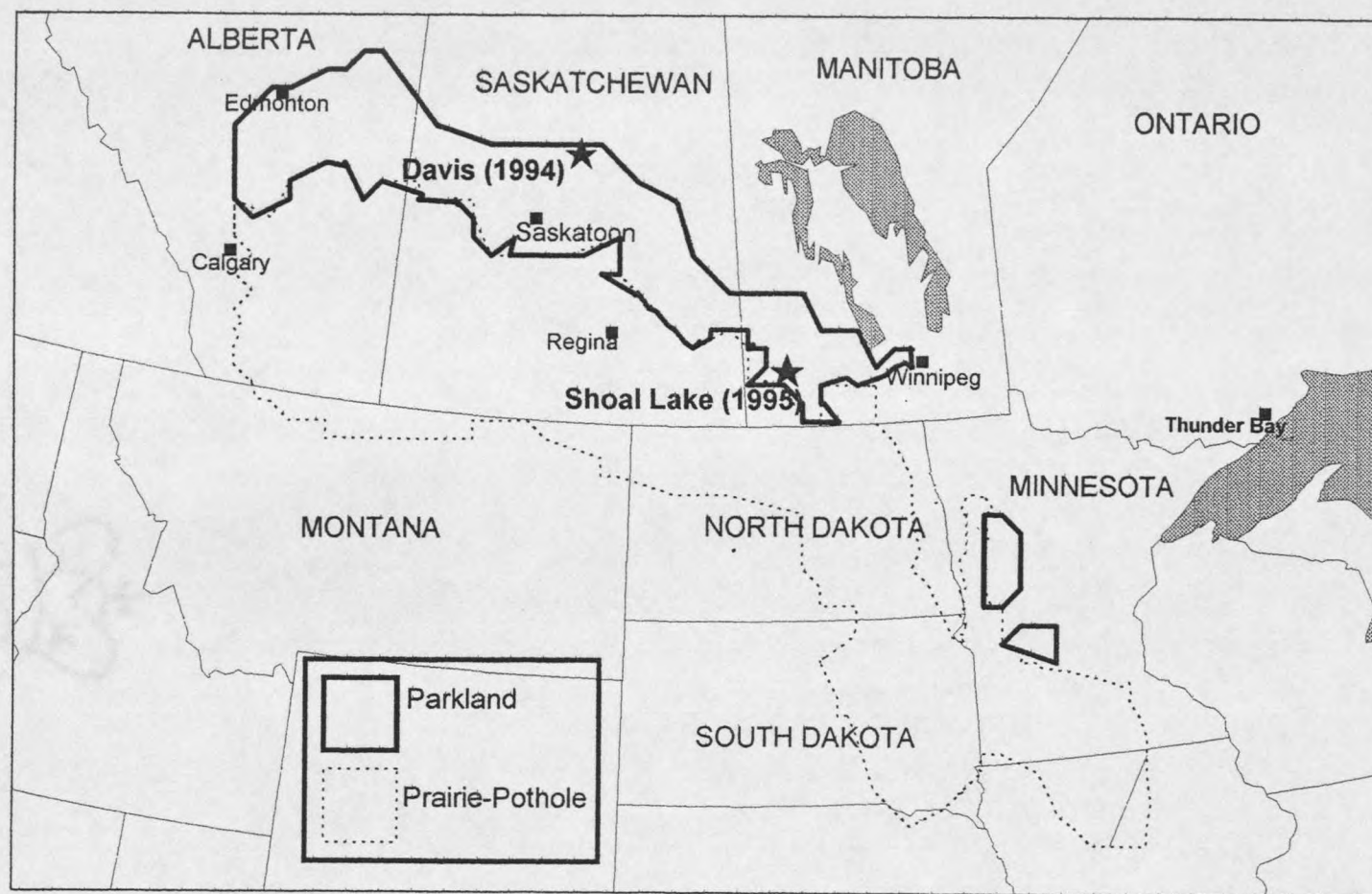


Figure 1. Locations of the Davis, Saskatchewan (1994) and Shoal Lake, Manitoba (1995) study areas.

(Table 1). Wetland sizes ranged from <0.01 ha to 1.5 ha, and wetland density averaged 68.2 wetlands/km². Treated habitat comprised 6% of the Davis study area and included planted dense nesting cover (DNC), cooperative programs to delay hay cutting until 15 July (delayed hay; prevents destruction of early nests caused by mowing), and existing idle cover not in immediate human use. The Davis study area had a density of 7.1 breeding pairs of mallards/km² (IWWR, unpubl. data). The average normal temperature during the breeding season (April-August) was 12.0 °C, and average normal precipitation for the same period was 49.6 mm. (Environment Canada, unpubl. data).

The Shoal Lake study area (20.5 km²) was located 7 km south of Shoal Lake, Manitoba (50° 22' N, 100° 36' W) in the Newdale Plain subregion of the parkland ecoregion (Poston et al. 1990). Topography was flat to gently rolling, and the area contained numerous and diverse wetlands (Table 1). Wetland sizes ranged from <0.01 ha to 15.6 ha, and wetland density averaged 30.7 wetlands/km². In addition to wetland basins, the study area also had a river and an associated tributary flowing through it. The Shoal Lake study area was a control site (no PHJV habitat treatments). However, there were several man-made nesting islands (with planted cover) in one permanent wetland. The study area had a density of 5.5 breeding pairs of mallards/km² (IWWR, unpubl. data). The average normal temperature during the breeding season (April-August) was 13.1 °C, and the average normal precipitation was 58.9 mm (Environment Canada, unpubl. data).

The native aspen-parkland habitat on both study areas has been largely replaced by intensive agriculture, primarily oil-seed and cereal grains, livestock forage production, and

Table 1. Spring characteristics of wetlands at Davis, Saskatchewan (1994) and Shoal Lake, Manitoba (1995).

Wetland Type (Class) ^a	Davis			Shoal Lake		
	n ^b	Area (ha) ^c	no./km ^{2d}	n ^b	Area (ha) ^c	no./ km ^{2d}
Tilled (T)	418	11.08	32.7	162	19.69	7.9
Ephemeral (1)	3	0.08	0.2	40	16.45	1.9
Temporary (2)	28	0.80	2.2	67	10.68	3.3
Seasonal (3)	238	55.21	18.6	274	135.48	13.4
Semipermanent (4)	183	170.14	14.3	65	106.24	3.2
Permanent (5)	3	0.17	0.2	17	44.56	0.8
Riverine	- ^e	-	-	3	33.51	0.2
Total	873	237.47	68.2	628	366.61	30.7

^a Wetland classes assigned following methods of Stewart and Kantrud (1971).

^b Sample size based on all visited wetlands on 12.8 km² (Davis) and 20.48 km² (Shoal Lake) areas.

^c Areas based on length and width measurements of basins taken in April and May and calculated using methods of Millar (1973).

^d Wetland density calculations based on data from 12.8 km² (Davis) and 20.48 km² (Shoal Lake) areas.

^e River habitat was not available at Davis.

pasture for beef cattle. Dominant habitat types on both study areas included cropland and grassland (Table 2). Land not in agricultural production included areas in wetland basins, small groves of aspen and poplar (*Populus* spp.), areas along fencelines, and small patches of grassland consisting of native and tame species. Willow (*Salix* spp.) and red-osier dogwood (*Cornus stolonifera*) dominated low lying areas around wetlands. Upland shrubs and understory species were typically wild rose (*Rosa woodsii*), snowberry (*Symphoricarpos albus*), serviceberry (*Amelanchier alnifolia*), chokecherry (*Prunus virginiana*), and silverberry (*Elaeagnus commutata*).

Important waterfowl predators (Sargeant et al. 1993) found on both study areas included: red foxes (*Vulpes vulpes*), striped skunks (*Mephitis mephitis*), raccoons (*Procyon lotor*), mink (*Mustela frenata*), American crows (*Corvus brachyrhynchos*), black-billed magpies (*Pica pica*), red-tailed hawks (*Buteo jamaicensis*), great-horned owls (*Bubo virginianus*), and northern harriers (*Circus cyaneus*).

Table 2. Habitat availability based on ground surveys and interpretation of aerial photos taken in July of 1994 and 1995 at Davis, Saskatchewan (1994) and Shoal Lake, Manitoba (1995) study areas.

Habitat Type Habitat Category ^a	Habitat Availability			
	Davis		Shoal Lake	
	Area (ha)	Proportion of study area	Area (ha)	Proportion of study area
Cropland	682.23	0.49	779.78	0.48
Growing crops	595.88	0.43	673.14	0.42
Fallow	86.35	0.06	66.86	0.04
Chemical fallow	- ^b	-	28.55	0.02
Grazed cropland	-	-	11.23	0.01
Grassland	323.13	0.23	272.15	0.17
Tame/mowed/right-of-ways	70.08	0.05	63.69	0.04
Native idle	0.27	0.00	11.09	0.01
Pasture	88.35	0.06	162.35	0.10
Hay	65.57	0.05	34.60	0.02
Delayed Hay	72.72	0.05	-	-
Planted Cover	26.14	0.02	0.42	0.00
Wood/Scrub	142.28	0.10	194.72	0.12
Woodland	57.05	0.04	87.03	0.05
Scrubland	62.56	0.05	79.05	0.05
Other ^c	22.67	0.02	28.64	0.02
Wetland^d	237.47	0.17	366.61	0.23
Total Area	1385.11	1.0	1613.26	1.0

^a Habitat categories were used in habitat selection analysis.

^b Habitat type not present on study area.

^c Includes: rockpiles, buildings, equipment, and unclassified miscellaneous habitats.

^d Includes all wetland classes within 12.8 km² (Davis) and 20.48 km² (Shoal Lake).

METHODS

Data Collection

Work was conducted at the Davis study area in 1994 and at the Shoal Lake study area in 1995. On each area, I used the following approach to study habitat selection and home range sizes of radiomarked female mallards: (1) I conducted wetland and upland surveys, entered data into a geographical information system (GIS), and calculated habitat availability with GIS software; (2) I trapped and radiomarked female mallards; (3) I estimated locations of radiomarked females using radio telemetry; (4) I assigned habitats to estimated locations using GIS software; (5) I calculated habitat use based on the GIS habitat assignments; (6) I compared habitat use to habitat availability; and (7) I estimated home range sizes using the estimated locations of radiomarked females.

Habitat Availability

Wetland availability was determined by censusing wetlands in April and May on 12.8 km² at Davis and on 20.5 km² at Shoal Lake. On both study areas, I revisited wetlands in late June and July to determine changes in wetland conditions using 1 of 2 sampling protocols. On the Davis study area, I revisited wetlands on 7 1.6-km diameter plots (14.1 km², some circles extended beyond study area boundary circular plots). I centered plots

on hatched nests of marked females so I could simultaneously collect data on changes in wetland habitat availability and on habitat availability for specific broods (Rotella and Ratti 1992). Low nesting success (IWWR, unpubl. data) prevented me from obtaining reasonable samples of brood-rearing females at Shoal Lake, and logistical constraints prevented me from re-censusing the entire study area again in July. Therefore, at Shoal Lake, I revisited all wetlands on 15.4 km² of the 20.5 km² study area. During each wetland survey, I recorded permanency class and type (Stewart and Kantrud 1971); dominant and sub-dominant emergent vegetation; width of flooded-emergent vegetation; length and width of flooded basin (used for area calculation, Millar 1973); and type of disturbance to the wetland (e.g., burned). At both study areas, I compared data from early and late wetland surveys to determine mid-summer wetland conditions (e.g., percent of dry basins).

I placed wetlands in the following categories: tilled, ephemeral/temporary, seasonal, semipermanent/permanent, and rivers. Permanency classes of tilled wetlands could not be determined because the characteristic vegetation needed to distinguish classes had been removed by agricultural activities (Stewart and Kantrud 1971). To reduce the number of habitat classes considered, I combined ephemeral and temporary wetlands and permanent and semipermanent wetlands.

I also calculated availability of upland habitats on the same areas used for initial wetland surveys. To reduce the likelihood of Type II errors in tests for habitat selection (Alldredge and Ratti 1986), several similar upland habitat types were combined prior to habitat-selection analysis. Upland habitats considered were: (1) cropland (growing crop,

summer fallow, chemical fallow, and idle cropland), (2) grass/hay (all native and tame, grazed and idle grasslands, hay, delayed hay, planted cover, and road and railroad right-of-ways), (3) wood/shrub (woody vegetation [trees and shrubs] with an areal coverage of >30%, and miscellaneous habitats [rock piles, hay bales, roads, farmyards, buildings]). I measured upland habitat availability from aerial photos taken in July of the year I worked on an area. I imported digitized photos into a GIS (IDRISI for Windows, Eastman 1995) and calculated the area of each upland habitat type using IDRISI's AREA procedure.

Capture and Marking

Pre-laying female mallards were captured with decoy traps (Sharp and Lokemoen 1987) during April and May 1994-95. Trapped females were weighed, measured, banded with USFWS aluminum leg bands, and implanted with abdominal transmitters (Telonics IMP/150; 22g). Surgery and implant techniques followed those of Olsen et al. (1992) as modified by Rotella et al. (1993).

Location Estimation

An assistant (Shoal Lake) and I (Davis and Shoal Lake) estimated locations of radiomarked female mallards using triangulation (White and Garrott 1990:90-94). Triangulations were conducted from a vehicle-mounted receiving system and a grid of roads that typically allowed for triangulations from ≤ 0.8 km. On both study areas, the road system was oriented north-south and east-west and formed a grid of roads with 1.6-

km (1-mi) spacing. Bearings to females were estimated from receiving stations placed along roads. Coordinates for each station were obtained using a global positioning system (GPS; differentially corrected to ≤ 3 m). Selection criteria for roadside receiving stations included the following: (1) high points along roads and (2) areas with good visibility into off-road habitats. Before estimating bearings to females, we aligned our telemetry vehicle parallel to a roadside and then stopped at a receiving station. We then used a null-antenna system (Kenward 1987) mounted on the roof of a truck and a compass-rose assembly mounted on the inside roof of the truck to estimate bearings to radiomarked females. At each stop, bearings were plotted on 1:10,000 aerial photo composites to assess triangulations. To increase detection of erroneous bearings and decrease error in estimating actual transmitter locations (White and Garrott 1990:58), we attempted to estimate ≥ 3 bearings per triangulation (see Results). We estimated 2 bearings to females that were on confirmed nests or in cases where ≥ 3 bearings could not be estimated (e.g., limited vehicle access). If plots of bearings indicated that a female had moved during any location estimation (e.g., the third bearing not converging with the intersection of the first 2 bearings), we started the location estimate over and triangulated to the new estimated location. If only 2 bearings were taken, we checked for transmitter movement by aiming the antennas toward the last estimated bearing for about 1 minute and monitoring the frequency for a variable signal that would indicate to us that the female was moving.

We estimated locations of each female 1-6 times per day from the date of marking until early-August. We estimated locations of every female each day between 0600 and 1300

hours throughout the study. We used this time period during the nesting period because this was when laying females were most likely to be on their nests (Gloutney et al. 1993). Knowledge of a female's nesting status was critical for assigning females to the appropriate reproductive stage (e.g., pre-nesting, nesting, post-breeding). To adequately sample habitat use and movements of females during afternoon and evening, I: (1) divided up the period of 1300-2200 hours into 3 3-hour blocks (I used 3-hour blocks because a complete circuit of location estimates for all radiomarked females took approximately 3 hours to complete.), (2) randomly selected 1-2 time period(s) to use each day, and (3) conducted 1 (1994) or 2 (1995) afternoon or evening circuits of location estimates for all females each day. Once per week during May through mid-July 1995, we also estimated 2 locations per female between 2200-0400 hours. To avoid obtaining locations on the same females at the same time each day, we began location estimates each day in a different quadrant of the study area. Estimated locations for each female were also separated by ≥ 1 hour to maintain independence of observations (Swihart and Slade 1985).

We attempted to see females whenever possible but generally were only able to do so when females were in roadside habitats. Females did not have external markers or antennas to aid in visual identification. Therefore, during all visual observations, females were first located with telemetry and then, by homing or triangulating, identified as radiomarked females. We recorded the following when a female was observed: date, time of day, habitat type, activity, breeding status (paired, alone, flocked), and location (for use in generating UTM's). I homed to radiomarked females with a hand-held yagi antenna when triangulations were impractical or could not be done (e.g., female in roadside habitat

but not visible because of emergent vegetation). Homing was accomplished by circling the area where a female was suspected to be and noting the habitat type.

I checked the accuracy of the telemetry system every 1-4 days by comparing estimated bearings to known bearings to radio beacons placed throughout each study area. If discrepancies between estimated and known bearings were found, I: (1) checked the positioning of the telemetry vehicle for proper road alignment and attempted the comparison again, and (2) if alignment was correct, I repositioned the compass-rose pointer to the correct bearing.

Habitat Use

We assigned estimated locations to habitats (see below) and investigated habitat use during 3 biological periods of the mallard breeding cycle: pre-nesting, egg production, and post-breeding. Because incubating females spent virtually all of their time on nests, I was not able to collect adequate samples of non-nesting location estimates for incubating females. Therefore, I did not estimate habitat use during incubation. Also, habitats used for nesting are the subject of PHJV research and were not considered in this study.

Because many females initiated multiple nests, the pre-nesting and egg-development periods each consisted of data associated with multiple nesting attempts for some females. The pre-nesting period began 3 days after a female was trapped (used to give birds time to recover from trapping and surgery), extended to the start of rapid-follicular growth (RFG, period of egg development beginning 6 days before the first egg in a clutch is laid

[Alisauskas and Ankney 1992:35-36]), and included all days between renesting attempts that females were not undergoing RFG (i.e., renesting periods >6 days). The egg-production period extended from the start of RFG to the date of clutch completion or nest destruction and included all days between renesting attempts that females were undergoing RFG (i.e., renesting periods ≤ 6 days). The post-breeding period began after a female's last nest was hatched or destroyed and continued until the bird left the area or the field season ended.

Home Range

To examine the sizes of areas used by females during various reproductive stages, I estimated home ranges for females during 3 distinct periods: (1) pre-laying, (2) nesting, and (3) post-breeding. Periods were slightly different from those used for habitat-use analysis because I wanted to examine how large an area was used prior to nesting (i.e., area from which nesting sites are chosen), during nesting (i.e., area monitored for possible renesting attempts), and after nesting. Also, estimating home range sizes for shorter periods (e.g., individual nest attempts) was not feasible due to sample size requirements. Thus, for home range analysis, the pre-laying period began 3 days after a female was decoy-trapped and extended to the day before her first egg was laid. The nesting period began on the day a female laid her first egg in her first nest and extended to the day her last nest was destroyed or hatched. The post-breeding period began after the last nesting attempt was completed and extended until signal transmission from a female's transmitter

was no longer detected or until the end of the study in August. During the post-breeding period, females were categorized as brood females or failed nesters.

Data Analysis

Accuracy of Location Estimates

I estimated the bias and bearing standard deviation of my telemetry system using bearings estimated to radiomarked females on nests with known coordinates (obtained from GPS) and a SAS program (SAS Inst., Inc. 1985) adapted from White and Garrott (1990:86). This approach was deemed appropriate because: (1) nests were found in a diversity of upland and wetland habitats throughout the study areas, (2) nests were located at a wide range of distances (10-1,400 m) from receiving stations, and (3) the observer was unaware at the time of bearing estimation of the true bearing to the females nest.

Location Estimation

The sample of locations of radiomarked females used to estimate habitat selection and home range sizes consisted of visual observations, location estimates produced by homing to females, and point estimates of locations produced by triangulations. For visual observations and locations estimated by homing, I used detailed field notes and GIS maps (1-m pixel resolution) to associate Universal Transverse Mercator (UTM) coordinates with each location. For locations estimated by triangulation, I only used locations

produced from a set of bearings estimated within a 25-minute period. I calculated maximum-likelihood estimates (MLE) of, and associated 95% error ellipses for, triangulated location estimates using bearings, the estimated standard deviation of bearings, and SAS code (SAS Inst., Inc. 1985) adapted from White and Garrott (1990:64).

Habitat Use

In heterogeneous habitats, the error ellipse formed by ≥ 3 bearings may contain several different habitat types, making assignment of a habitat to the location estimate difficult. White and Garrott (1990:200) reviewed 3 possible solutions to this problem: (1) eliminate all such locations, (2) randomly assign the location to one of the habitats within the ellipse, or (3) use the habitat in which the estimated point location falls. White and Garrott (1990:200) judged the estimated-point-location approach acceptable as long as some habitat types do not cause signal bounce and bias point estimates of locations. Both study areas consisted of 88-90% open habitat, and thus, signal bounce should have been minimal (Hupp and Ratti 1983). Therefore, I used point estimates (MLE's) of locations when assigning each estimated location to a single habitat type (White and Garrott 1990:200, Podruzny 1996).

To assign habitats to location estimates, I entered the point estimates into GIS vector files, overlaid the files on digital maps of the study areas, and extracted the habitat type for each estimated location using IDRISI's EXTRACT procedure (Eastman 1995).

I compiled the total number of different wetlands used by each female with ≥ 14 location estimates per reproductive period. To test for changes in the number of wetlands used in different periods and on different study areas I conducted ANOVA with PROC GLM (SAS Inst. Inc. 1985). If significant interactions between period and study area were found, averages for the number of wetlands used in each reproductive period on each study area were compared using Tukey's Honest Significant Difference (HSD) comparison tests for unequal sample sizes ($P \leq 0.05$).

Habitat Use Versus Availability

Within each reproductive period, I pooled habitat-use data from all females with ≥ 14 estimated locations and used Johnson's preferred rank test (1980) to determine whether female mallards were using habitats in proportion to their availability. I calculated habitat availability proportions using wetland habitat taken from initial wetland surveys and upland habitat taken from IDRISI study area images. I used program PREFER 5.1 (Pankratz 1994) to calculate average preference ranks in each reproductive period on each study area and to test for significant differences between preference ranks ($P \leq 0.05$) using multiple comparisons (Waller and Duncan 1969). Simulations by Alldredge and Ratti (1986) suggest that Johnson's method performs well (Type I and II error rates of 5% and 20%, respectively) for the number of habitat categories used and number of observations per animal obtained in this study.

Home Range

I estimated home range size with the adaptive-kernel estimator because Worton (1989, 1995) has shown that this method lacks many of the problems associated with other home range estimators. The polygon method (Odum and Kuenzler 1955), which has been used in previous mallard studies, can create home range estimates that are highly correlated with the number of estimated locations per animal and that contain non-utilized habitats (White and Garrott 1990). Although using the adaptive-kernel estimator limits my ability to compare my results with previous studies using the polygon method, my approach does allow comparison of individual variation among females.

Adaptive kernel home range estimates were calculated using with the program CALHOME (Kie et al. 1996). I selected bandwidth and grid-cell size following methods presented by Kie et al. (1994). For each female with ≥ 20 location estimates in a reproductive period, I calculated the 100% (maximum home range) and 50% (core area) probability contours in that reproductive period. I tested for changes in home range size in different reproductive periods and on different study areas using PROC GLM (SAS Inst. Inc. 1985). I conducted ANOVA and tested for main effects of reproductive period and study area and for interactions between period and study area. If significant interactions were found, averages for home range sizes in different reproductive periods and study areas were compared using Tukey's HSD comparison tests for unequal sample sizes ($P \leq 0.05$) to determine which means differed among reproductive periods and study

areas. I also used PROC GLM (SAS Inst. Inc. 1985) to test for changes in the number of estimated locations used in different periods and on different study areas.

I investigated relationships between home range size and reproductive performance and survival by using several methods. First, I compared average 100% home range size in each reproductive period to the total number of nests per female using simple linear regression. Second, I used a *t*-test ($P \leq 0.05$) to compared the average 100% home range size in each period for females that survived the breeding season with those that did not. Finally, I compared the average 100% home range size in each period for successful females (females that hatched a nest) and unsuccessful females (*t*-test, $P \leq 0.05$).

RESULTS

Habitat-use and home range data were collected on 57 female mallards (29 at Davis, 28 at Shoal Lake). During the study, 21 females died (9 at Davis, 12 at Shoal Lake), 14 females had transmitters that failed or left the study areas (12 at Davis, 2 at Shoal Lake), and 22 females survived and were monitored successfully throughout a breeding season, 7 at Davis, 15 at Shoal Lake. Reproductive periods varied in duration according to each individual female's physiological schedule, and not all females were represented during each period. I obtained an average of 2.24 locations per female per day (SE = 0.16, range = 1.5-4.2) on the Davis site and 3.24 locations per female per day (SE = 0.15, range = 2.6-4.4) on the Shoal Lake site.

Habitat Availability

During 1994 and 1995, the average amount of precipitation received on each study area from April-August was 70.5 mm (30% above normal) and 66.6 mm (12% above normal), respectively (Environment Canada, unpubl. data). Although both study areas had above average precipitation, Shoal Lake wetlands responded more dramatically by flooding out of their basins and into adjacent uplands. Average temperatures from April-August 1994 and 1995 were 12.3° C (normal = 12.0° C) and 12.4° C (normal = 13.1° C), respectively (Environment Canada, unpubl. data).

Both study areas contained diverse wetlands (Table 1), and virtually all basins contained water in April and May (Figure 2). However, a greater variety of wetland classes held water later in the season at Shoal Lake than at Davis. In July 1994, 68% of 517 re-visited wetlands were dry, whereas only 30% of 497 wetlands re-visited in July 1995 were dry. Further, 97 to 100% of basins in tilled, ephemeral, and temporary classes were dry in July 1994, whereas 63-72% of such basins were dry in July 1995 (Figure 2). Similarly, 64% of seasonal basins were dry in July 1994, whereas only 8% of such basins were dry in July 1995 (Figure 2). Permanent wetlands, which on both sites consisted mostly of dug-outs for livestock watering, and most semipermanent wetlands remained full throughout both study years.

Accuracy of Location Estimates

I calculated bearing standard deviations of 5.22° (average = -0.20° , $n = 125$) and 4.33° (average = 0.57° , $n = 111$) for my telemetry system on the Davis and Shoal Lake study areas, respectively. Although most were small ($\leq 10^\circ$) (Davis, 94%; Shoal Lake, 99%), large ($>10^\circ$) bearing errors (Davis, $n = 8$; Shoal Lake, $n = 1$) were present on both study areas and ranged from 10.4° - 14.4° . Average 95% error-ellipse sizes for Davis and Shoal Lake were $24,756 \text{ m}^2$ (SE = 691, $n = 1,923$) and $39,044 \text{ m}^2$ (SE = 944, $n = 3,356$), respectively. Given the heterogeneous nature of habitat on the study areas, ellipses typically encompassed several habitat types.

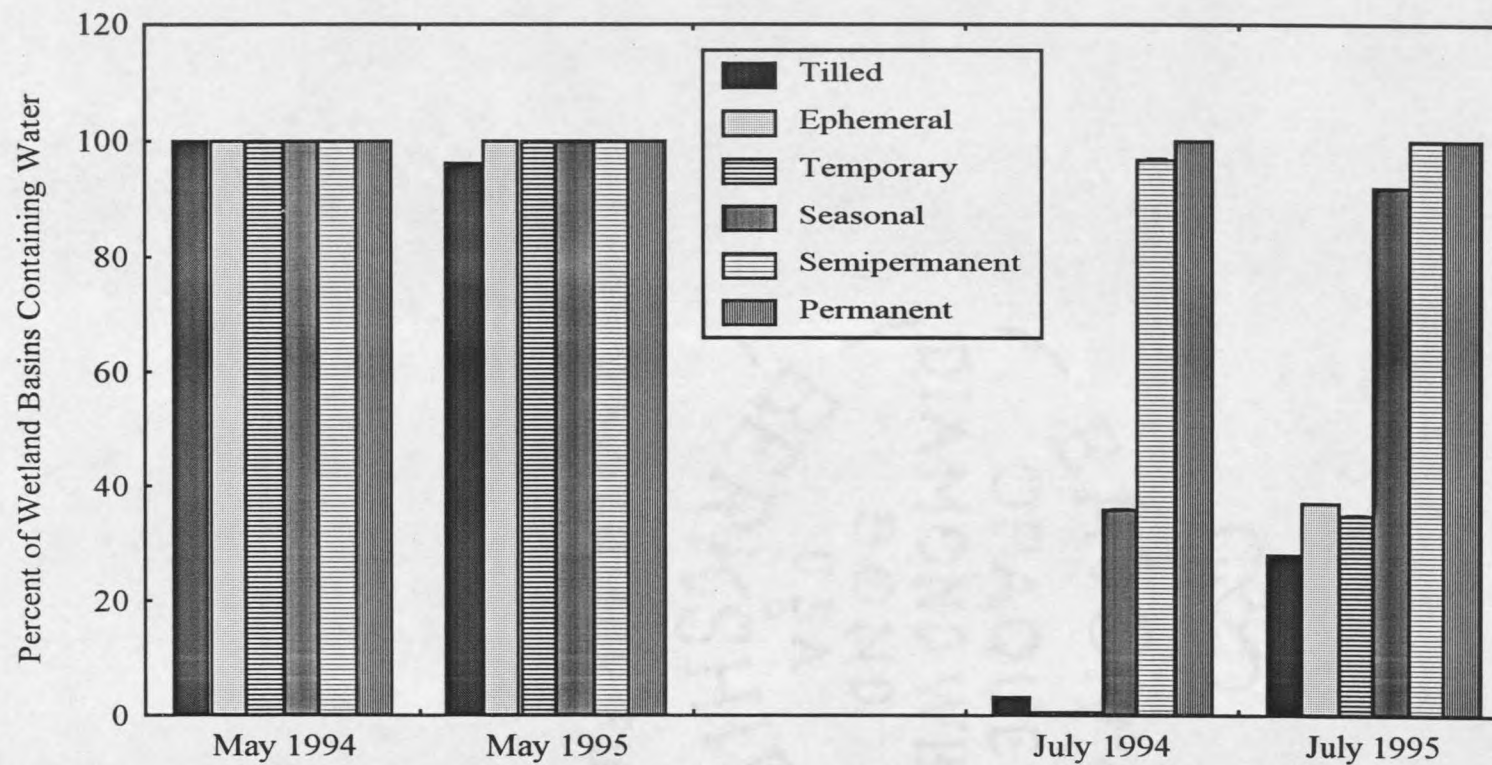


Figure 2. Percentage of wetland classes containing water in May and July at Davis, Saskatchewan (1994) and Shoal Lake, Manitoba (1995).

Habitat Use

I estimated 1,925 female locations at Davis and 3,770 at Shoal Lake. On the Davis study area, the average number of location estimates per female during pre-nesting, egg-production, and post-breeding periods were: 39.1 (SE = 7.4, $n = 14$), 33.8 (SE = 3.5, $n = 22$), and 38.4 (SE = 6.2, $n = 11$), respectively. On the Shoal Lake study area, the average number of location estimates per female during pre-nesting, egg-production, and post-breeding periods were: 72.5 (SE = 12.2, $n = 24$), 78.5 (SE = 7.4, $n = 18$), and 51.3 (SE = 5.1, $n = 12$), respectively.

Females used an average of 6.7 to 15.3 wetlands during different reproductive periods on the 2 study areas (Table 3). The number of wetlands used within a period ranged from 1 wetland per female to 35 wetlands per female. There was a significant interaction between the effects of reproductive period and study area on the number of wetlands used by a female ($F = 4.43$; 2, 93 df; $P = 0.01$). At Davis, the average number of wetlands used did not differ among reproductive periods ($P \geq 0.98$) (Table 3). At Shoal Lake, however, the number of wetlands used was greater in the egg-production than in the post-breeding period ($P = 0.04$). The average number of wetlands used on different study areas, but during the same reproductive period, was not different during the pre-nesting ($P = 0.12$) or post-breeding period ($P = 0.99$). However, during the egg-production period females used more wetlands at Davis than at Shoal Lake ($P = 0.0004$).

Table 3. Average number of wetlands used by female mallards in various reproductive periods at Davis, Saskatchewan (1994) and Shoal Lake, Manitoba (1995).

Reproductive Period	Number of Wetlands Used						<i>P</i> ^b
	Davis			Shoal Lake			
	n ^a	Average	SE	n ^a	Average	SE	
Pre-nesting	14	7.00 A ^c	0.69	24	12.54 AB ^c	1.11	0.12
Egg production	22	6.73 A	1.01	18	15.28 A	2.07	0.0004
Post-breeding	11	8.38 A	0.94	10	7.70 B	2.12	0.99

^a Number of radiomarked females monitored per period on each study area.

^b Significance levels for comparisons made between study areas within a reproductive period. Tukey's HSD test for unequal *n* ($P \leq 0.05$) was used to compare averages after ANOVA detected a significant interaction between period and study area ($F = 4.43$; 2, 93 df; $P = 0.01$)

^c Significance levels for comparisons made among periods within a study area. Averages followed by the same letter within columns were not significantly different (Tukey's HSD test for unequal *n*, $P \leq 0.05$).

The estimated amount of time females spent in various habitat types was similar among all periods at Davis. However, at Shoal Lake I found that females varied their habitat use among periods. Based on data from all periods, females were found in upland habitats 39-49% of the time at Davis and 12-27% of the time at Shoal Lake. Cropland had the highest use of any upland habitat on both study areas and among all periods (Davis - 24-26%; Shoal Lake - 4-13%) followed by grassland (Davis - 9-12%; Shoal Lake - 4-9%) and woodland/scrubland/other (Davis - 4-7%; Shoal Lake - 4-6%) habitat categories (Table 4). Not surprisingly, females were found in wetland habitats more (>50%) than upland habitats on both study areas and among all periods. Use of semipermanent/permanent wetlands was among the highest use levels on both study areas and among all periods and varied from 39-49% at Davis and 26-36% at Shoal Lake (Table 4). Females appeared to use seasonal wetlands less at Davis (8-11%) than at Shoal Lake (16-34%). On both study areas and in all periods, females were found in tilled wetlands between 5-11% of the time and made little use of ephemeral/temporary wetlands (0-3%). At Shoal Lake, use of riverine habitat was low (4-6%) during the pre-nesting and egg-production periods. However, post-breeding females were found in riverine habitat 29% of the time (Table 4).

Habitat Use versus Availability

Females on both study areas and during all reproductive periods preferred wetland habitats to upland habitats ($P \leq 0.05$). However, individual wetland classes were not

Table 4. Proportional habitat use of, and available habitat for, radiomarked female mallards at Davis, Saskatchewan (1994) and Shoal Lake, Manitoba (1995).

Study Area	Habitat Category ^a	Proportion of Available Habitat ^b	Proportion of Habitat Use by Reproductive Period		
			Pre-nesting	Egg Production	Post-breeding
Davis	Cropland	0.4926	0.24	0.25	0.26
	Grassland	0.2333	0.12	0.12	0.09
	Wood/Scrub	0.1027	0.07	0.07	0.04
	Tilled	0.0080	0.05	0.06	0.05
	Ephemeral/Temporary	0.0006	0.01	0.01	- ^c
	Seasonal	0.0399	0.10	0.11	0.08
	Semi-permanent/Permanent	0.1230	0.41	0.39	0.49
Shoal Lake	Cropland	0.4834	0.13	0.12	0.04
	Grassland	0.1687	0.07	0.09	0.04
	Wood/Scrub	0.1207	0.06	0.06	0.04
	Tilled	0.0122	0.11	0.06	0.07
	Ephemeral/Temporary	0.0168	0.03	0.02	0.01
	Seasonal	0.0840	0.24	0.34	0.16
	Semi-permanent/Permanent	0.0935	0.32	0.26	0.36
	Riverine	0.0208	0.06	0.04	0.29

^a Habitat categories that were used in habitat analysis.

^b Available habitat is based habitats within 12.8 km² (Davis) and 20.5 km² (Shoal Lake).

^c No locations estimated to be ephemeral/temporary wetlands at the Davis study area.

preferred equally among all reproductive periods or among study areas ($P \leq 0.05$) (Figure 3). At Davis, females preferred: (1) all wetlands equally during the pre-nesting period; (2) tilled, semipermanent/permanent, and seasonal wetlands during the egg-production period; and (3) semipermanent/permanent and tilled wetlands during the post-breeding period ($P \leq 0.05$) (Figure 3). At Shoal Lake, females preferred: (1) seasonal and tilled wetlands during the pre-nesting and egg-production periods and (2) riverine habitat, and tilled and seasonal wetlands during post-breeding ($P \leq 0.05$) (Figure 3). Females showed no preference for upland habitats on either study area or in any period ($P \leq 0.05$) (Figure 3).

Home Range

I used 2,555 (Davis) and 4,547 (Shoal Lake) location estimates to estimate home range sizes. (The number of estimated locations was larger for home range calculation than for habitat-selection analysis because home range estimates also included nest site locations.) At Davis, the average numbers of location estimates per female during pre-laying, nesting, and post-breeding periods were: 47.1 (SE = 7.4, $n = 14$), 79.2 (SE = 8.3, $n = 19$), and 43.4 (SE = 6.5, $n = 9$), respectively. At Shoal Lake, the average numbers of location estimates per female during pre-laying, nesting, and post-breeding periods were: 78.9 (SE = 14.0, $n = 21$), 124.7 (SE = 12.4, $n = 18$), and 54.6 (SE = 5.6, $n = 10$), respectively.

Davis

	SEMI	TILL	SEAS	EPH	WOOD	CROP	GRSS
Pre-nesting							
Ranks	-1.25	-1.21	-1.14	-0.71	0.61	1.50	2.21
Egg Prod.	TILL	SEMI	SEAS	EPH	WOOD	CROP	GRSS
Ranks	-1.27	-1.14	-0.64	-0.55	0.45	1.27	1.86
Post-breeding	SEMI	TILL	SEAS	EPH	WOOD	CROP	GRSS
Ranks	-1.86	-1.31	-0.68	-0.59	1.00	1.36	2.09

Shoal Lake

	SEAS	TILL	SEMI	EPH	RIV	WOOD	CROP	GRSS
Pre-nesting								
Ranks	-2.96	-2.31	-1.48	-0.44	0.04	1.88	2.45	2.81
Egg Prod.	SEAS	TILL	SEMI	EPH	RIV	WOOD	CROP	GRSS
Ranks	-3.31	-2.28	-1.08	-0.53	0.78	1.83	1.89	2.69
Post-breeding	RIV	SEAS	TILL	SEMI	EPH	WOOD	GRSS	CROP
Ranks	-3.05	-2.05	-1.50	-0.90	-0.30	1.65	2.75	3.40

Figure 3. Female mallard habitat preference from available habitat at Davis, Saskatchewan (1994), and Shoal Lake, Manitoba (1995) using Johnson's (1980) preferred ranks method. Habitats sharing an underline were not different ($P \geq 0.05$). Rank is the average difference among ranks. Negative ranks indicate preference for a particular habitat, positive ranks indicate no preference. SEMI = Semi-permanent/Permanent wetlands, TILL = Tilled wetlands, SEAS = Seasonal wetlands, EPH = Ephemeral/Temporary wetlands, WOOD = Woodland/Scrubland, CROP = Cropland, GRSS = Grassland, RIV = Rivers.

There was a significant interaction between the effects of reproductive period and study area on the size of average 100% home ranges ($F = 3.70$; 2, 85 df; $P = 0.03$). The average home range size did not differ between reproductive periods on either study area ($P \geq 0.35$) (Table 5). However, average 100% home ranges were significantly larger ($P = 0.005$) at Shoal Lake during the pre-laying period than during the same period at Davis. Contrary to results for 100% home range sizes, there was no interaction between the effects of reproduction and study area on the size of core areas ($F = 0.92$; 2, 85 df; $P = 0.40$), and there were no significant main effects of reproductive period ($F = 1.04$; 2, 85 df; $P = 0.36$). However, the main effect of study area was significant ($F = 8.71$; 1, 85 df; $P = 0.004$): core areas were significantly larger at Shoal Lake than at Davis (Table 5).

I did not find a linear relationship between average 100% home range sizes and number of nesting attempts during the pre-laying period (Davis: $R^2 = 0.03$, $P = 0.53$; Shoal Lake: $R^2 = 0.04$, $P = 0.40$), but there was a weak relationship on both study areas within the nesting period (Davis: $R^2 = 0.18$, $P = 0.08$; Shoal Lake: $R^2 = 0.17$, $P = 0.08$). Average home-range sizes for unsuccessful versus successful females were not different during pre-laying (Davis - $P = 0.44$; Shoal Lake - $P = 0.12$) or nesting periods (Davis - $P = 0.64$; Shoal Lake - $P = 0.29$). Similarly, average home range sizes were not different during pre-laying (Davis - $P = 0.10$; Shoal Lake - $P = 0.91$) or nesting periods (Davis - $P = 0.50$; Shoal Lake - $P = 0.82$) for females that survived a breeding season versus those that died during a breeding season.

Table 5. Average home range sizes using 100% and 50% adaptive-kernel probability contours of radiomarked female mallards at Davis, Saskatchewan (1994) and Shoal Lake, Manitoba (1995).

Contour Size Reproductive Period	Davis			Shoal Lake			<i>P</i> ^c
	<i>n</i> ^a	Average ^b (ha)	SE	<i>n</i> ^a	Average ^b (ha)	SE	
100%							
Pre-laying	14	147.88 A	36.67	21	1563.21 A	352.17	0.005
Nesting	19	193.94 A	47.29	18	917.21 A	295.39	0.27
Post-breeding	9	400.03 A	201.62	10	666.23 A	188.76	0.99
50%							
Pre-laying	14	7.04	2.33	21	37.98	9.77	-
Nesting	19	7.08	2.96	18	21.64	7.13	-
Post-breeding	9	14.91	7.70	10	30.70	9.97	-

^a Number of females with relocations ≥ 20 providing home-range information.

^b Averages followed by the same letter within columns were not significantly different using Tukey's HSD test for unequal *n* ($P \leq 0.05$). Average 50% contours were significantly larger in 1995 ($F = 8.28$; 2, 85 df; $P > 0.000$), and there were no significant effects of reproductive period ($F = 0.89$; 2, 85 df; $P = 0.41$).

^c Significance levels for comparisons made between years within a reproductive period. Tukey's HSD test for unequal *n* ($P \leq 0.05$) was used to compare averages after ANOVA detected significant interaction between period and year for 100% average home-range size ($F = 3.70$; 2, 85 df; $P = 0.03$).

DISCUSSION

Habitat Use

Given life-history strategies of mallards, it was not surprising that females spent most of their time in wetland habitats. It was surprising, however, that despite within-year temporal changes in physiological needs of females and in habitat availability, I only observed 1 seasonal change in the number of wetlands used. On the Shoal Lake study area females used more wetlands during egg production than in the post-breeding period. Females may have used fewer wetlands during the post-breeding period at Shoal Lake simply because fewer wetlands held water by mid-summer. Alternatively, post-breeding females may have been attracted to larger, more-stable wetlands when they were molting wing feathers and preparing for fall migration. Finally, female awareness of available habitat might have been such by the post-breeding period that exploration of wetlands was unnecessary and wetland use was restricted to the few necessary basins.

Interestingly, despite differences in habitat composition on the 2 areas, I only found differences in the number of wetlands used during 1 period. During the egg-production period, females used more wetlands at Shoal Lake than at Davis. One reason for the observed difference could be that individual wetlands provided fewer resources on the Shoal Lake study area. During egg production, females rely heavily on animal protein to

develop eggs. If wetlands were of poorer quality, females may have needed to visit more wetlands to meet protein needs during egg development. Although the Shoal Lake site had a lower percentage of tilled wetlands than the Davis site (i.e., lower human disturbance to wetlands), most wetlands were flooded during early season. This natural disturbance may have disrupted invertebrate food sources, or increased depths such that invertebrates were less available or unattainable. Unfortunately, I was unable to collect invertebrate population data, which would have allowed me to evaluate hypotheses about factors influencing wetland use. Competitive release might provide another possible explanation for why birds used more wetlands at Shoal Lake. However, this explanation does not seem plausible because mallard density was similar on the 2 areas (Davis - 7.1 breeding pairs of mallards/km²; Shoal Lake - 5.5 breeding pairs of mallards/km²). Dwyer et al. (1979) and Krapu et al. (1983) looked at changes in wetland use by nesting female mallards, but their research was done in areas of low wetland densities (1-12 wetlands/km²) and primarily during dry years. Thus, their results do not seem to apply well to my results. Clearly, data from replicate years and multiple areas along with invertebrate data are needed to better understand the mechanisms responsible for patterns of wetland use. Also, I caution that other differences may have been present among periods or between study areas but gone undetected because of high among-female variation.

Even though nest-site data were not included in habitat-use calculations, females still spent 4-26% of their time in uplands. Thus, uplands may have provided important resources to females. However, telemetry may have overestimated the use of uplands and

underestimated the use of habitats with smaller areas. My estimates may be biased high because large error-ellipse sizes and the prevalence of upland habitat on each area may have caused numerous point estimates of female locations to erroneously fall in uplands. However, I did regularly see females resting and feeding in uplands. Dwyer et al (1979) also reported that females used uplands, especially croplands, regularly (23% of the time). Of course, their estimate may also be biased due to radio-telemetry error. Further research is needed to identify whether key resources are obtained in uplands. Such study will be difficult, however, until telemetry accuracy and the ability to confirm upland locations greatly improves.

Although seasonal wetlands were abundant at Davis, females did not spend as much time on seasonal wetlands (8-11%) on the Davis study area as they did in previous studies (Stewart and Kantrud [1973] - 44%, Dwyer et al. [1979] - 45%). It is not clear why use was lower at Davis. However, despite lower use of seasonal wetlands in my study, females did display selection for seasonal wetlands (see below). Thus, seasonal wetlands still appear to be important to female mallards. Future field studies should collect data on wetland characteristics such as depth, cover attributes, and invertebrate levels. Such data would allow multivariate analyses, which might provide insights into reasons for differences in use patterns observed on different study areas.

Habitat Use versus Availability

On the Davis study area, when high densities of tilled, seasonal, and semipermanent wetlands were available, I found that pre-nesting females preferred all wetland classes containing water and did not prefer any one wetland class more than another. In contrast, on the Shoal Lake study area, when only seasonal wetlands were available in high densities, pre-nesting females preferred seasonal wetlands significantly more than wetlands with lower densities. Despite differences in habitat selection between the 2 sites, females were able to renest (Davis - average = 1.8 nests per female; Shoal Lake - average = 3.0 nests per female; IWWR unpubl. data). Thus, my findings suggest that female mallards are able to adapt their patterns of habitat use according to habitat availability to meet reproductive needs.

Ephemeral and temporary wetlands may provide critical food resources to females upon their arrival in early spring when larger wetlands are still frozen. However, based on my findings, shallow wetlands, which have been especially impacted by drainage, were important, but no more important than other wetland types. Habitat selection does not directly measure the criticalness of a habitat to an animal (White and Garrott 1990:198). Future studies should investigate reproductive success and survival of females breeding on areas with or without ephemeral and temporary wetlands to evaluate whether these habitats are critical (White and Garrott 1990:198).

Previous studies concluded that seasonal wetlands are important to breeding mallard females (e.g., Swanson et al. 1985). My findings confirm the importance of seasonal

wetlands, which were preferred during the pre-nesting and egg-production periods, to females requiring high levels of nutrients for egg development. At Davis, however, when seasonal wetlands were available in high densities, they were not preferred more than wetlands in other classes. Thus, other wetland types may be just as important to breeding mallards as seasonal wetlands in some areas/years and should be considered in habitat planning. Again, future studies should investigate criticalness of seasonal wetlands with perturbation experiments of the type suggested for ephemeral and temporary wetlands (White and Garrott 1990:198).

On both study areas, females changed their habitat preferences as the breeding season progressed in accordance with their changing needs. Despite the fact that many seasonal wetland basins still contained water in July 1994, post-breeding females preferred semipermanent wetlands over seasonal wetlands. At Shoal Lake, females selected riverine habitat during the post-breeding period despite not exhibiting preference for riverine habitat during pre-nesting and egg-production periods. Given their large areal extent and high water permanency, semipermanent wetlands and riverine habitat likely provided secure cover, reliable food sources, and stable habitats for molting and pre-migratory females.

Habitat preferences are based on habitat use and habitat availability. In this study, habitat use may have been biased because telemetry errors may have resulted in misclassification of estimated locations and biased preference results. Because mallards generally are found along the edges of wetlands while feeding and resting, overestimation of use of highly available upland habitats might be expected. However, uplands were not

preferred during any period on either study area, which may indicate that the misclassification rate was low.

To better understand the habitat features related to habitat selection, future studies of habitat selection should collect data on multiple study areas in replicate years. Multivariate analysis of factors related to wetland preference would be particularly useful. Also, it would be useful to obtain large enough samples of use data for each female such that analysis of data for individual females could be accomplished (e.g., Aebischer et al. 1993). This is important because analysis of pooled data sets may indicate that females are habitat generalists when, in fact, females are specialists with various individual preferences (e.g., Rotella and Ratti 1992).

Home Range

Analysis of home ranges indicated that females were quite variable in terms of the size of the area they used regularly. The variation was not well explained by time of year or study area. Rather, within each period and on each study area, females were quite variable with respect to home range size (e.g., Shoal Lake pre-laying home range = 170.5-7154.0 ha; average = 1563.21 ha). Similar levels of variation have been reported by previous studies (Dwyer et al. 1979, range = 306.6-718.9 ha; Kirby et al. 1985, range = 40-1440 ha). Thus, variation in home range size seems common to females on all areas studied despite distinct landscape differences among study areas used (north-central Minnesota forest, Kirby et al. [1985]; North Dakota prairies, Dwyer et al. [1979]; Canadian

Parklands, this study). (Note: because previous studies used different analysis methods to estimate home range than I used in this study, home ranges used in comparisons of estimates from this study with those from previous studies should be interpreted with caution.)

During this study, home range size did not differ between pre-nesting and nesting periods despite the fact that females had quite different requirements during these 2 periods, i.e., pre-nesting females were searching for suitable nest sites and seeking out nutritional requirements to satisfy the energy demands of egg development. In contrast, Gilmer et al. (1975) found that female mallards in a forested area of Minnesota reduced their home ranges from an average of 135 ha during pre-nesting to 70 ha during laying and 58 ha during incubation. I may have failed to find a difference between the 2 periods because I included data for all re-nesting attempts when calculating nesting home ranges for females. My results and those of Kirby et al. (1985) indicate that nesting home ranges tend to increase in size with each additional nesting attempt.

Post-breeding home range sizes were highly variable (sedentary to highly mobile) during this study. Gilmer et al. (1977) also found that individual post-breeding females varied in their movements. On their study area, females left areas lacking large permanent wetlands, and many were later found on lakes and rivers elsewhere in Minnesota. In my study, females that were unsuccessful nesters typically joined flocks shortly after their last nesting attempt, although several remained solitary. At Davis, most females left the study area shortly after joining flocks of conspecifics, presumably to find larger wetland areas

before undergoing molt. In contrast, at Shoal Lake, flocked females remained on the area and centered their activities on riverine or permanent wetlands.

Core areas (50% home range estimates) showed similar patterns of variation to that seen in 100% home range estimates. However, despite the fact that 100% home range sizes were similar on my 2 study areas, core areas were larger at Shoal Lake. Several factors may explain why core areas were larger at Shoal Lake. Habitat quality may have been lower at Shoal Lake, which caused females to use larger areas to satisfy their nutritional needs (Krapu et al. 1983). Although I did not directly measure habitat quality, data on nesting effort indicate that females on both study areas were able to adequately meet their nutritional needs (average number of days devoted to nesting = 35.3 at Davis, 47.1 at Shoal Lake). Thus, once again my data indicate that female mallards were quite plastic in their strategy for obtaining critical resources. Another possible explanation for larger core areas at Shoal Lake might be related to density of conspecifics (i.e., less competition) (Titman 1983). Titman (1983) found that territory sizes decreased when the number of mallard breeding pairs/km² increased from 4-8 mallard breeding pairs/km² to 22-25 mallard breeding pairs/km². However, this explanation seems implausible for my data because the differences in the density of mallard breeding pairs/km² on my 2 study areas were minimal (7.1 pairs/km² at Davis; 5.5 pairs/km² at Shoal Lake). Finally, wetland density may have affected the size of core areas. Dwyer et al. (1979) suggested that females on a semi-arid North Dakota study area had large home ranges because wetland densities were low and females were required to move farther to satisfy breeding requirements. This explanation may have some merit for my data: although both areas had

high wetland densities, densities were substantially lower at Shoal Lake (30.7 wetlands/km²) than at Davis (68.2 wetlands/km²). Thus, females may have been required to increase their movements to satisfy all of their breeding requirements on the Shoal Lake study area. It is important to note, however, that annual differences in home range sizes may have been confounded by differences in sampling effort between study areas. That is, the larger home range sizes found at Shoal Lake may reflect the fact that more locations per female were obtained on that study area.

It was somewhat surprising that pre-nesting home range sizes and core areas were larger at Shoal Lake, yet, measures of reproductive output (e.g., days devoted to nesting and re-nesting attempts) were similar to those at Davis. Females with larger home ranges likely expended more energy while meeting their daily energy requirements and may be expected to have to reduce reproductive output accordingly. However, females may alternatively simply feed for a greater proportion of each day to make up for the extra energy consumption associated with larger home ranges. Unfortunately, no behavioral observations, time budgets, or energetics studies were conducted to test this assumption.

Investigation into differences in home range sizes for successful (e.g., those that hatched a nest) and unsuccessful females indicated that no pattern was present. Similarly, there was no difference between home range sizes for females that survived the study and those that were killed during the study. This is not to suggest that home range size causes success or failure, or higher survival or mortality rates. These results simply indicate that individual females can achieve similar reproductive success via different strategies.

MANAGEMENT AND RESEARCH IMPLICATIONS

Females used a variety of wetland types and, in some cases, a large number of wetlands. Further, habitat selection differed somewhat among periods and between study areas. Thus, not surprisingly, given the unpredictable nature of mallard breeding habitat, my data suggest that mallards are habitat generalists. Data for other aspects of the mallard breeding cycle lend further support to this assertion: (1) mallards have the most extensive breeding range of any North American duck (Bellrose 1980:231); (2) mallard nests are found in a wide variety of habitats (e.g., Cowardin et al. 1985, Greenwood et al. 1987); and (3) mallard broods act as habitat generalists (Rotella and Ratti 1992). Given the diverse strategies used by mallards, habitat plans should strive to preserve/create wetland complexes with a high number and diversity of wetlands. Data from this study indicate that intensive habitat treatments (e.g., dense nesting cover) should be centered every 1.4-4.5 km (calculations based on the diameter of a circular version of the average pre-laying home range size and assume home range overlap of individual females.) on managed areas to ensure that all females on the area are exposed to such treatments. However, wetland density, diversity, and spatial arrangement of habitats likely influence home range size and therefore, the spatial arrangement of habitat treatments may need to vary accordingly. For example, at Davis, pre-laying home range sizes were smaller, possibly due to higher wetland densities. Therefore, on the Davis study area, habitat treatments based on pre-

laying home range sizes (circular home range: 1.4-km diameter) would need to be centered every 1.4 km to expose about 11 breeding mallard pairs to this treatment (7.1 breeding mallard pairs/ $\text{km}^2 \times$ average pre-laying home range of 1.48 km^2). Shoal Lake had lower wetland densities (30.7 wetlands/ km^2) than Davis (68.2 wetlands/ km^2) and average home range size was larger during the pre-laying period (circular home range: 4.5-km diameter). Distances between habitat treatments on the Shoal Lake site would be approximately 4.5 km apart and have the potential to expose about 88 breeding mallard pairs to treatments (5.5 breeding mallard pairs/ $\text{km}^2 \times$ average pre-laying home range of 15.68 km^2). However, nesting success and recruitment rates were much lower at Shoal Lake and consideration of competing covers (Johnson et al. 1987), nesting success in various treatment types, and recruitment from treatment types should be evaluated before expensive habitat treatments are implemented.

Because I only completed 1 year of work on each study area, further replication is needed to evaluate hypotheses regarding factors influencing habitat selection and movements and the population consequences of variation in habitat selection and movements. Multiple-year studies would better address the range of variation observed during this study. Study areas should include landscapes that represent areas in which the PHJV plans habitat improvements. In addition, because landscape disturbances are common in the prairie-parkland region, a variety of study areas should be selected, ranging from undisturbed areas (e.g., native communities still largely intact) to highly disturbed areas (e.g., high human impact to uplands and wetlands).

The high observed variability among females may have been the result of variation in female age, available habitat, and/or habitat juxtaposition. Thus, future studies should collect data on such factors, and consider invertebrate abundance and various wetland characteristics, and conduct multivariate analyses of factors related to habitat selection. Adequate sample sizes should be obtained to allow analysis of individual birds. Wetland densities and diversities vary by area and year throughout the prairie-parkland region, thus, relationships between habitat selection and home range size should be investigated between areas and during years of high and low wetland densities and diversities. Furthermore, coinciding invertebrate studies should be conducted on all study areas and in each replicate year so explanations of use and movements could be supported with these data.

LITERATURE CITED

- Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313-1325.
- Alisauskas, R. T. and C. D. Ankney. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl. Pages 30-61 *in* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, eds. The ecology and management of breeding waterfowl. Univ. Minnesota Press, Minneapolis.
- Anonymous. 1987. Prairie habitat: a prospectus. Prairie Habitat Joint Venture Advisory Board. Ducks Unlimited Canada, Winnipeg, Manit. 32pp.
- Anonymous. 1994. Ducks Unlimited Continental Conservation Plan, Parts I-III. Ducks Unlimited, Inc., Memphis, Tenn. 379pp
- Aldredge, J. R., and J. T. Ratti. 1986. Comparison of some statistical techniques for analysis of resource selection. *J. Wildl. Manage.* 50:157-165.
- Ball, I. J., D. S. Gilmer, L. M. Cowardin, and J. M. Reichmann. 1975. Survival of wood duck and mallard broods in north-central Minnesota. *J. Wildl. Manage.* 39:776-780.
- Baydack, R. K., J. H. Patterson, C. Rubec, A. Tyrchniewicz, and T. W. Wiens. 1995. Management challenges for Canadian prairie grasslands in the 21st century. *Trans. N. Amer. Wildl. and Nat. Resour. Conf.* 60:386-396.
- Bellrose, F. C. 1980. Ducks, geese and swans of North America. 3rd ed. Stackpole Books, Harrisburg, Pa. 543pp.
- Canadian Wildlife Service and U.S. Fish and Wildlife Service. 1986. North American waterfowl management plan: a strategy for cooperation. U.S. Dept. of Interior. Washington, D.C. 19pp.
- ____ and _____. 1994. 1994 update to the North American waterfowl management plan: expanding the commitment. U.S. Dept. of Interior. Washington, D.C. 30pp.
- ____ and _____. 1996. Waterfowl population status, 1996. U. S. Fish and Wildl. Serv. Off. Migr. Bird Manage., Washington, D.C. 40pp.
- Clark, R. G., and T. D. Nudds. 1991. Habitat patch size and duck nesting success: The crucial experiments have not been performed. *Wildl. Soc. Bull.* 19:534-543.
- ____, D. S. Gilmer, and C. W. Shaiffer. 1985. Mallard recruitment in the agricultural environment of North Dakota. *Wildl. Monogr.* 92. 37pp.

- Dwyer, T. J., G. L. Krapu, and D. M. Janke. 1979. Use of prairie pothole habitat by breeding mallards. *J. Wildl. Manage.* 43:526-531.
- Duebbert, H. F., J. T. Lokemoen, and D. E. Sharp. 1983. Concentrated nesting of mallards and gadwall on Miller Lake Island, North Dakota. *J. Wildl. Manage.* 47:309-321.
- Dzubin, A. 1955. Some evidences of home range in waterfowl. *Trans. N. Amer. Wildl. Conf.* 20:278-298.
- Eastman, J. R. 1995. IDRISI for Windows: user's version 1.0. Clark Univ., Grad. School of Geog., Worcester, Mass.
- Gilmer, D. S., I. J. Ball, L. M. Cowardin, J. H. Riechmann, and J. R. Tester. 1975. Habitat use and home range of mallards breeding in Minnesota. *J. Wildl. Manage.* 39:781-789.
- _____, R. E. Kirby, I. J. Ball, and J. H. Riechmann. 1977. Post-breeding activities of mallards and wood ducks in north-central Minnesota. *J. Wildl. Manage.* 41:345-359.
- Gloutney, M. L., R. G. Clark, A. D. Afton, and G. J. Huff. 1993. The timing of nest searches for upland nesting waterfowl. *J. Wildl. Manage.* 57:597-601.
- Greenwood, R. J., A. B. Sargeant, D. H. Johnson, L. M. Cowardin, and T. L. Shaffer. 1987. Mallard nest success and recruitment in prairie Canada. *Trans. N. Amer. Wildl. and Nat. Resour. Conf.* 52:298-309.
- _____, _____, _____, _____, and _____. 1995. Factors associated with duck nest success in the Prairie Pothole Region of Canada. *Wildl. Monogr.* 128. 57pp.
- Hupp, J. W., and J. T. Ratti. 1983. A test of radio telemetry triangulation accuracy in heterogeneous environments. *Proc. Int. Wildl. Biotelem. Conf.* 4:31-46.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology.* 6:65-71.
- _____, D. W. Sparling, and L. M. Cowardin. 1987. A model of the productivity of the mallard duck. *Ecol. Model.* 38:257-275.
- Kantrud, H. A., and R. E. Stewart. 1977. Use of natural basin wetlands by breeding waterfowl in North Dakota. *J. Wildl. Manage.* 41:243-253.
- Kenward, R. E. 1987. Wildlife radio tagging. Academic Press, San Diego, Calif. 222pp.

- Kie, J. G., J. A. Baldwin, and C. J. Evans. 1994. CALHOME: Home range analysis program electronic user's manual. USFS, Fresno, Calif.
- _____, _____, and _____. 1996. CALHOME: a program for estimating animal home ranges. *Wildl. Soc. Bull.* 24:342-344.
- Kirby, R. E., J. H. Riechmann, and L. M. Cowardin. 1985. Home range and habitat use of forest-dwelling mallards in Minnesota. *Wilson Bull.* 97:215-219.
- Kirsch, A. T., H. F. Duebbert, and A. D. Kruse. 1978. Grazing and haying effects on habitats of upland nesting birds. *Trans. N. Amer. Wildl. and Nat. Resour. Conf.* 43:486-497.
- Klett, A. T., T. L. Shaffer, and D. H. Johnson. 1988. Duck nest success in the prairie pothole region. *J. Wildl. Manage.* 52:431-440.
- Krapu, G. L., and C. R. Luna. 1991. Habitat use, survival, and causes of mortality among mallard broods hatched near the James River in North Dakota. *Prairie Nat.* 23:213-222.
- _____, A. T. Klett, and D. G. Jorde. 1983. The effect of variable spring water conditions on mallard reproduction. *Auk* 100:689-698.
- LaGrange, T. G., and J. J. Dinsmore. 1989. Habitat use by mallards during spring migration through central Iowa. *J. Wildl. Manage.* 53:1076-1081.
- Millar, J. B. 1973. Estimation of area and circumference of small wetlands. *J. Wildl. Manage.* 37:30-38.
- Mulhern, J. H., T. D. Nudds, and B. R. Neal. 1985. Wetland selection by mallards and blue-winged teal. *Wilson Bull.* 97:473-485.
- Odum, E. P., and E. J. Kuenzler. 1955. Measurement of territory and home range size in birds. *Auk* 72:128-137.
- Olsen, G. H., F. J. Dein, G. M. Haramis, and D. G. Jorde. 1992. Implanting radio transmitters in wintering canvasbacks. *J. Wildl. Manage.* 56:325-328.
- Orthmeyer, D. L., and I. J. Ball. 1990. Survival of mallard broods on Benton Lake National Wildlife Refuge in northcentral Montana. *J. Wildl. Manage.* 54:62-66.
- Pankratz, C. 1994. Preference assessment program PREFER, IBM PC Version 5.1. Northern Prairie Science Center, Jamestown, N.D. 11pp.

- Podrutzny, K. M. 1996. Radiotelemetry error: factors affecting bearing error and the ultimate effects of triangulation error on determining habitat use. M. S. Thesis, Mont. State Univ., Bozeman. 104pp.
- Pospahala, R. S., D. R. Anderson, and C. J. Henny. 1974. Population ecology of the mallard II. Breeding habitat conditions, size of the breeding populations and production indices. U.S. Fish and Wildl. Serv. Resour. Publ. 115. 73pp.
- Poston, B., D. M. Ealey, P. S. Taylor, and G. B. McKeating. 1990. Priority migratory bird habitats of Canada's prairie provinces. Canadian Wildlife Service, Edmonton. 107pp. and map.
- Rotella, J. J. and J. T. Ratti. 1992. Mallard brood movements and wetland selection in southwestern Manitoba. J. Wildl. Manage. 56:508-515.
- _____, D. W. Howerter, T. P. Sankowski, and J. H. Devries. 1993. Nesting effort by wild mallards with 3 types of radio transmitters. J. Wildl. Manage. 57:690-695.
- Sargeant, A. B., R. J. Greenwood, M. A. Sovada, and T. L. Shaffer. 1993. Distribution and abundance of predators that affect duck production-Prairie Pothole Region. U.S. Fish and Wildl. Serv. Resour. Publ. 194. 96pp.
- SAS Institute Inc. 1985. SAS procedures guide for personal computers. Version 6 edition. SAS Inst., Cary, N.C. 373pp.
- Sharp, D. E., and J. T. Lokemoen. 1987. A decoy trap for breeding-season mallards in North Dakota. J. Wildl. Manage. 51:711-715.
- Stewart, R. E., and H. A. Kantrud. 1971. Classification of natural ponds and lakes in the glaciated prairie region. U.S. Fish and Wildl. Serv. Resour. Publ. 92. 57pp.
- _____ and _____. 1973. Ecological distributions of breeding waterfowl populations in North Dakota. J. Wildl. Manage. 37:39-50.
- Stoudt, 1971. Ecological factors affecting waterfowl production in the glaciated prairie region. U.S. Fish and Wildl. Serv. Resour. Publ. 99. 58pp
- Swanson, G. A., M. I. Meyer, and V. A. Adomaitis. 1985. Foods consumed by breeding mallards on wetlands of south-central North Dakota. J. Wildl. Manage. 49:197-203.
- Swihart, R. K., and N. A. Slade. 1985. Testing for independence of observations in animal movements. Ecology 66:1176-1184.

- Talent, L. G., G. L. Krapu, and R. L. Jarvis. 1982. Habitat use by mallard broods in south central North Dakota. *J. Wildl. Manage.* 46:629-635.
- Titman, R. D. 1983. Spacing and three-bird flights of mallards breeding in pothole habitat. *Can. J. Zool.* 61:839-847.
- Turner, B. C., G. S. Hochbaum, F. D. Caswell, and D. J. Nieman. 1987. Agricultural impacts on wetland habitats on the Canadian prairies, 1981-85. *Trans. North Am. Wildl. Nat. Resour. Conf.* 52:206-215.
- Waller, R. A., and D. B. Duncan. 1969. A bayes rule for the symmetric multiple comparisons problem. *J. Am. Stat. Assoc.* 64:1484-1503.
- White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, Calif. 383pp.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home range studies. *Ecology* 70:164-168.
- _____. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *J. Wildl. Manage.* 59:794-800.

